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Rates of inbreeding and genetic adaptation for populations managed as herds in zoos with a rotational mating system or with optimized contribution of parents

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Summary

This study compares two genetic management scenarios for species kept in herds, such as deer. The simulations were designed so that their results can be extended to a wide range of zoo populations. In the first scenario the simulated populations of size 3x20, 6x40 or 20x60 (herds x animals in herd) were managed with a rotational mating (RM) scheme in which 10%, 20% or 50% of males were selected for breeding and moved between herds in a circular fashion. The second scenario was based on optimal contribution theory (OC). OC requires an accurate pedigree to calculate kinship; males were selected and assigned numbers of offspring in order to minimize kinship in the next generation. RM was efficient in restriction of inbreeding and produced results comparable with OC. However, RM can result in genetic adaptation of the population to the zoo environment, in particular when 20% or less males are selected for rotation and selection of animals is not random. Lowest rates of inbreeding were obtained by combining OC with rotation of males as in the RM scheme. RM is easy to implement in practice and does not require pedigree data. When full pedigree is available, OC management is preferable.

Keywords: optimal contribution, rotational mating, breeding circle, zoo populations

Introduction

Maintenance of genetic diversity is particularly important for small populations of wild animals maintained in zoo gardens. Currently zoos have a rich portfolio of breeding programs

that includes more than 500 species survival plan (SSP) programs managed by Association of Zoos and Aquariums (AZA 2014), and 388 European Endangered species Programs (EEP) and the European StudBook (ESB) programs managed by European Association of Zoos and Aquaria (EAZA 2014). The aim of these programs is to make every effort to ensure that genetic diversity of captive populations is maintained. The key in this case is to maintain adequate genetic and demographic structure, which will ensure steady growth of the population over many generations (Lees & Wilcken 2009). Cooperation is indispensable here as many zoo populations are isolated and too small to conduct a balanced breeding program (Lees & Wilcken 2009).

The aim of every genetic conservation program is to minimize the loss of genetic diversity, and to control rates of inbreeding as much as possible. However, some reports (Earnhardt et al. 2001; Zimmermann et al. 2007) suggest that a number of breeding programs in zoos achieve sub-optimal results. According to Long et al. (2011) the median of gene diversity retained for 264 SSP populations is 92% and it is predicted to fall to 67% in 100 years. It is also worth mentioning that 38% of the AZA populations retain less than 90% of genetic diversity of the founding populations (Long et al. 2011). This points to the need to optimize breeding programs to better manage available resources. Past methods proposed for conservation of genetic diversity included tools that affect mating strategies such as maximum avoidance of inbreeding (Wright 1921), which can be efficient in the short term but may result in high inbreeding in the long term (Caballero & Toro 2000), and tools to maintain genetic diversity like population fragmentation and breeding in isolated herds to conserve genetic diversity on the meta-population level (Leus et al. 2011). However, the latter strategy is not recommended for small herds as inbreeding will rapidly increase, resulting in inbreeding depression and accumulation of deleterious alleles (Whiteley et al. 2015). Currently, mating of animals based on mean kinship is the main method used for

management of zoo populations (Leus et al. 2011). Mean kinship is the mean of the kinship coefficients of a given individual with every individual in the population including itself. Priority is given to matings of animals with low mean kinship as they have few relatives in the population and are likely to carry alleles that are rare in the population (Ballou & Lacy 1995). Determination of parents and their contributions to the next generation has to be followed by a decision on how to mate the animals. This can be achieved through a two-step approach, where first contributions are allocated to the animals and subsequently mating pairs are optimised (Fernandez & Caballero 2001; Sonesson & Meuwissen 2000), or a single-step approach that optimises both parameters at the same time (Ballou & Lacy 1995; Fernandez et al 2001). Fernandez et al. (2001) evaluated performance of both methods using simulations and concluded that the amount of genetic diversity preserved by the two methods was quite similar, but the single-step method was more flexible and assured compatibility between the contributions of males and females. This should therefore lead to overall higher levels of genetic diversity. A more recent simulation study by Ivy & Lacy (2012) explored the above mentioned mating strategies with an additional layer of complexity such as variable mortality rate, reproductive rate, pairing success rate and reproductive success rate. As a result dynamic mean kinship strategy (two-step approach) was recommended as optimal for populations of mammals with low fecundity and long lifespans (Ivy & Lacy 2012).

Implementation of kinship-based management poses several difficulties that are related to the limitations of zoo breeding programs. Zoo populations usually have a very limited capacity that restricts the number of animals which can be kept in the population. Therefore, to maintain the populations in good condition and avoid overcrowded zoo environment, it is necessary to either transfer part of the animals to another zoo or to cull them. Transferring of animals can also pose a significant challenge particularly if the animals that would form optimal mating pairs are from two distant locations. Therefore it is important to take into

account fragmentation of the population and organise the transfer of animals that limits the costs and effort involved. Additionally, with species such as deer or many other hoofstock animals, it is important to account for skewed reproduction rates. Because of hierarchical structure, few dominant males mate with groups of females and have high contributions, whereas the majority of males have very low or zero contributions to the next generation.

The best known strategy to maintain genetic diversity is by optimizing the contributions of the parents to minimize global kinship in their offspring (optimal contribution theory; (Meuwissen 1997). In livestock this method is used to optimize genetic gain while simultaneously restricting the rate of inbreeding. However, efficiency of this method depends strongly on pedigree completeness (Oliehoek & Bijma 2009). It has been demonstrated that with pedigrees containing gaps or misidentified parents the method does not perform well (Oliehoek & Bijma 2009). Low quality of pedigree information in populations of livestock and zoo animals is a common problem (Earnhardt et al. 2004; Oliehoek & Bijma 2009). Incorrect entries in pedigrees are usually impossible to detect without the use of molecular markers. In case of livestock, the level of pedigree errors reported in the literature is around 10% (Oliehoek & Bijma 2009), which can decrease efficiency of the optimal contribution method.

On the other hand there are methods, such as rotational mating, which do not require accurate pedigree records to control the increase of inbreeding (Nomura & Yonezawa 1996). Rotational mating occurs in several forms, but the basic idea is that females are mated with males coming from a different herd in a “round robin fashion”. Breeding circle, used especially in sheep breeding, is one of the most common forms of rotational mating. It is based on the strategy that each herd never uses its own males for breeding. Exchange of males between herds is performed in a rotational way. The first herd provides males for the second herd, the second herd provides males for the third, etc., and the last herd is the source

120 of males for the first herd (Windig & Kaal 2008). Possible errors or missing information in
121 the pedigrees do not affect performance of the method. Moreover, it can be used even in the
122 absence of pedigree data under the condition that it is possible to determine the herd of origin
123 for each animal.

124 Captive breeding programs usually aim to preserve the population so that it can be
125 reintroduced into the wild in the future (Frankham et al. 2010; Frankham 2015). The success
126 of such reintroduction widely depends on the level of wild fitness that has been preserved in
127 captivity. The mechanism of genetic adaptation to the captive environment is driven by
128 natural selection. Because zoo environments differ from the wild, the genetic variants that
129 confer the highest fitness in captivity differ from those that are beneficial in natural
130 environment (Frankham 2008). Genetic adaptation to captivity increases with selection
131 differential, genetic diversity, effective population size and generations in captivity
132 (Frankham 2008). Therefore it is important to avoid unintentional selection for characteristics
133 related to exterior appearance of the animal or personal preference of program coordinators.
134 This can be easily achieved in genetic management programs that are based on kinship, such
135 as optimal contribution theory, as it does not involve phenotypic selection, apart from natural
136 selection. On the other hand, some degree of unintentional phenotypic selection can occur
137 when only part of the animals are selected.

138 In this paper we use deer species maintained in zoos as an example to compare two strategies
139 to manage their genetic diversity. Deer populations in zoos are characterized by
140 fragmentation of the meta-population over several herds, skewed mating ratios ranging from
141 1 to 5 males per 10 females, and high variance in offspring among males caused by dominant
142 males in the herds. A recent analysis of studbooks of 15 deer species in European zoos
143 showed that most studbooks were incomplete, and that 10 out of 15 populations (species) had
144 low effective population size (between 10 and 20) with significant effect of inbreeding on

longevity and survival of offspring (Mucha, unpublished results). This points to the need for more effective management programs. In theory, breeding circles could offer a simple alternative to pedigree-based management for deer populations as deer are similar to sheep populations in a number of ways such as low reproductive rate of females, division in herds and males with highly variable number of offspring. Therefore, the aim of this paper was to compare performance of genetic management by rotational mating (breeding circles) with management based on pedigree and optimal contributions in simulated populations of deer. The simulations were designed in such a way that implications of the results could be extended to a wide range of zoo populations of animals with similar live histories and demographics.

Materials and Methods

Simulated populations

Three populations were simulated that resembled small populations of deer maintained in zoos in Europe. They were divided into herds resembling the actual number of zoos that bred each population. The first was a large population (based on *Elaphurus davidianus*) consisting of 1200 individuals per generation, divided over 20 herds (60 animals per herd). The second population (based on *Cervus eldii thamin*) consisted of 240 animals, divided in 6 herds (40 animals per herd), and the third (*Axis calamianensis*) of only 60 individuals kept in three herds (20 animals per herd). In each of the simulated populations half of the animals born each generation were male and half were female. For simplicity it was assumed that animals reproduced only once in a lifetime and died afterwards (discrete generations). Furthermore, to maintain a constant population size in each generation, it was assumed that each female gave

birth to two offspring: two males, two females, or one male and one female. The average sex ratio of all offspring (population level) in each generation was 1:1. There was no selection in females as they all had to participate in the creation of the next generation in order to maintain a constant population size. For each population, three mating ratios were simulated, where all females were used along with only 50% (1:2 mating ratio), 20% (1:5 mating ratio) or 10% (1:10 mating ratio) of males. Using only 10, 20, or 50% of the available males implies that (unintentional) selection could take place, which could lead to genetic adaptation. We therefore simulated two scenarios: one with random selection of males, and one with selection of males on a single (not specified) trait with a heritability of 0.3 and phenotypic variance of 1. The effect of inbreeding depression on the simulated trait was not included in the simulation.

Simulations were performed for 20 generations, and replicated 50 times.

All founders had a phenotypic value of 0 and a genetic value calculated as:

$$r_{norm}\sqrt{h^2\sigma_P^2}$$

where: r_{norm} is a random number drawn from a normal distribution with a mean of 0 and variance of 1, h^2 is the heritability (0.3), and σ_P^2 is the phenotypic variance of the simulated trait. In every generation, each offspring was assigned a genetic value *A* as follows:

$$A = \tfrac{1}{2}A_S + \tfrac{1}{2}A_D + \mathrm{MS}$$

where A_S and A_D are genetic values of sire and dam, respectively. Mendelian sampling term (MS) was calculated as:

$$\mathrm{MS} = r_{norm}\sqrt{\tfrac{1}{2}\left(1-\tfrac{1}{2}\left(F_s + F_D\right)\right)h^2\sigma_P^2}$$

where F_S and F_D are inbreeding coefficients of sire and dam, respectively. Phenotypic value of offspring was assigned as:

$$P = A + r_{norm}\sqrt{\left(1-h^2\right)\sigma_P^2}$$

Rotational mating (RM)

Breeding circles with discrete generations were used. In every generation the first herd provided male offspring for mating with females from the second herd. The second herd supplied males to the third herd et cetera. Female offspring remained in the same herd where they had been born. Two scenarios were considered for selection of males (Table 1). In the first scenario (1a), males were chosen at random (random selection) and rotated to the neighbouring herd, where they were used for breeding. The number of selected males depended on the mating ratio assumed (1:2, 1:5 or 1:10). Selected males were mated at random with females. Non-selected males did not reproduce. In the second scenario (1b) selection of males was based on their phenotype for the simulated trait (phenotypic selection). Males with the highest trait values were selected and rotated to the neighbouring herds, where they were mated at random with females.

Optimal contribution (OC)

The software package Gencont with the option "*minimise ΔF*" (Meuwissen 1997; Meuwissen, 2002) was used to determine the optimum contributions of animals to the next generation in order to achieve the lowest possible rate of increase in mean pairwise kinship. This was achieved by varying the contribution of each animal to the next generation (fraction of offspring attributable to the parent) according to the equation:

213 $$\min\left(\bar{A}_p\right) = \mathbf{c}'\mathbf{A}\mathbf{c}$$

214 where $\bar{A}_p$ is the lowest possible average relationship of parents; **c** is a vector of contributions
215 of length n (n = the total number of animals in the population); **A** is a relationship matrix of
216 selection candidates. The contributions of the selection candidates **c** are optimized by the
217 Lagrangian multiplier method. The $\bar{A}_p$ value has to increase over generations due to finite
218 population size which leads to increase of relationships over time.

219 In order to maintain constant population size, all females (N_f) were selected and received
220 equal contributions of $1/N_f \cdot 100\%$ Selection was performed only on the male side and their
221 contributions differed depending on their relatedness. The process was optimised so that for a
222 given number of males required for breeding (determined by the mating ratio) a set of males
223 was selected that would minimise kinship in the next generation, and their contributions were
224 varied to achieve the optimal result. The population was managed purely on kinship, thus
225 genetic gain was not expected.

226 With optimal contribution, three alternative management scenarios were considered (Table
227 1). In the first scenario it was assumed that mating was performed in a meta-population
228 without any subdivision into herds. Therefore selection and contribution of males based on
229 the optimal contribution theory was applied on a meta-population scale (OC_m). In the second
230 scenario, selection and mating was performed separately within each herd. There was no
231 exchange of animals between the herds (OC_i). The third scenario was similar to the optimal
232 contribution performed separately within each herd, but each generation males were
233 exchanged between herds in a rotational fashion similar to a breeding circle (OC_r).
234 Contributions of sires and dams to the next generation were calculated assuming all sires
235 from the neighbouring herd had been transferred to the herd of destination. Effectively, the
236 number of sires rotated between the herds was equal to the number of sires with nonzero

237 contributions. In every scenario, three mating ratios (1:2, 1:5 and 1:10) were simulated and
238 selected males mated with randomly chosen females. The mating ratio determined the
239 number of males with nonzero contributions selected by GENCONT in the optimal
240 contribution based scenarios, i.e. a mating ratio of 1:2 in pop3 means that 15 out of 30 sires
241 were selected to contribute to the next generation.

242

243 **Calculation of parameters**

244 The mean coefficient of inbreeding in each generation ($\overline{F_t}$) was calculated as:

245 $$\overline{F_t} = \frac{\sum_{i=1}^{N_t} F_i}{N_t}$$

246 where: F_i is the inbreeding coefficient of the i-th individual from generation *t*, N_t is the
247 number of individuals born in generation *t*

248 Increase of inbreeding per generation was calculated as:

249 $$\Delta F_t = \frac{\overline{F}_t - \overline{F}_{t-1}}{1 - \overline{F}_{t-1}}$$

250 Where: $\overline{F}_t$ and $\overline{F}_{t-1}$ are the mean inbreeding coefficients of the whole population in
251 generation *t* and *t-1*, respectively.

252 Mean increase of inbreeding in generations 5 to 20 was calculated as:

253 $$\Delta F = 1 - \sqrt[15]{\frac{1 - F_{20}}{1 - F_5}}$$

To allow for good comparison between rotational mating and optimal contribution selection schemes, generation 5 was used as starting point assuming that the population had reached Bulmer equilibrium.

Across population mean kinship in each generation was calculated as:

$$\overline{\mathrm{mk}}_t = \frac{1}{N_t}\sum_{i=1}^{N_t} mk_i = \frac{1}{N_t^2}\sum_{i=1}^{N_t}\sum_{j=1}^{N_t} f_{ij}$$

where: mk_i is the mean coefficient of kinship of the i-th individual with the rest of the population, f_{ij} is kinship between individuals *i* and *j* and N_t represents the total number of individuals born in the whole population in a given generation. Mean kinship within individual herds was calculated using the same formula, with N_t equal to the nuber of individuals born in each herd in a given generation.

Phenotypic mean was calculated as an arithmetic mean of trait values observed in a given generation. The mean genetic level was an arithmetic mean of breeding values for the simulated trait in a given generation.

Results

Rate of Inbreeding (ΔF)

Rate of inbreeding over time: as expected, in all schemes that used rotational mating (RM and OCr), inbreeding rates were zero in generations 1 and 2, and at a fairly constant level thereafter (Figure 1). Inbreeding rates in OCi and OCm schemes increased after generation 1, and fluctuated across generations, especially in small populations (e.g. 60 animals, see Figure 1).

Effects of population size and mating ratio: for each scheme tested, rates of inbreeding increased almost linearly with increasing mating ratio (Table 2). Inbreeding rate was highest in the smallest population (3x 20 animals) where the mean ΔF ranged from 0.71% to 2.20% (mating ratio 1:2) or from 3.11% to 10.99% per generation (mating ratio 1:10). As the population size increased the mean ΔF decreased (Table 2), irrespective of scheme. Lowest rates of inbreeding were recorded in the biggest population (20 x 60 animals), ranging from 0.03% to 0.72% at mating ratio 1:2 and from 0.14% to 3.09% at mating ratio 1:10.

Effect of management scheme: lowest rates of inbreeding were obtained when managing the meta-population with optimal contribution (OCm). Rates of inbreeding <1% could be achieved in populations with 240 and 1200 animals, for each mating ratio. In the smallest population (60 animals), achieving a rate of inbreeding <1% was only possible with a mating ratio of 1:2 (Table 2). In contrast, the highest rates of inbreeding were realized when managing the populations with optimal contribution in isolated herds. In the smallest population (3x20), rate of inbreeding ranged from 2.20% to 10.99% when managed with 1:2 and 1:10 mating ratio, respectively. Mean ΔF was smaller in the larger populations, but still mostly above the 1% threshold (Table 2).

Rotational exchange of sires between the herds, managed with (OCr) or without optimal contribution (RM), produced very similar results. Rates of inbreeding were always below 1% per generation (Table 2), except for the smallest population, managed with mating ratios of 1:5 or 1:10.

Kinship

The mean kinship of generation 20, calculated across herds, was very similar for all management schemes. Mean kinship increased with mating ratio and decreased with

population size. Lowest across mean kinship (0.01) was observed in the population with 1200 animals, divided over 20 herds. The highest values (0.30-0.49) were observed in the 3x20 population with a 1:10 mating ratio.

Managing isolated herds with optimal contribution, without exchange between herds (OCi), resulted in individual herds becoming very distinct from each other. Therefore, the 'across' mean kinship of the whole population was lower in comparison to the other management schemes, while the 'within' mean kinship was highest, ranging from 0.15 (20x60; mating ratio 1:2) to 0.91 (3x20; mating ratio 1:10) (Table 2).

The mean kinship (within and across) of generation 20 was very similar for RM and OCr schemes. Due to the exchange of males, herds were more connected than in the previous scenario (OCi) which led to a higher mean kinship of the whole population.

Inbreeding rate in RM schemes with and without unintentional selection

Performance of rotational mating schemes was also evaluated in additional simulations where we assumed unintentional directional selection for a single simulated trait. The results of this analysis indicate that rotational mating schemes with or without selection produce very similar mean inbreeding rates in all of the analysed populations, irrespective of mating ratio (Table 3). However, selection for a moderately heritable trait leads to substantial increase in genotypic values, up to 2 or more standard deviations from the founder mean, even in small populations (Table 3). For the larger populations, this is in line with what can be theoretically expected from phenotypic selection with selected proportions of 10% - 50%, a heritability of 0.3 and a phenotypic standard deviation of 1.

Discussion

Research on effective methods to reduce inbreeding in small zoo populations is particularly important in the light of recent reports stating that many of the current conservation programs do not meet the established demographic and genetic assumptions, which may threaten their survival or adversely affect the health of animals (Lacy 2013; Leus et al. 2011). The main problem according to Lacy (2013) is that many of the endangered populations have a limited availability of candidates for selection and low pedigree completeness. Therefore methods that can mitigate these problems are of particular value for zoo populations. Use of rotational mating schemes has been evaluated for small breeds of cattle (Colleau & Avon 2008), and sheep (Windig & Kaal 2008). Optimal contribution has also been studied as a tool to manage livestock populations (Avendaño et al. 2003; Koenig & Simianer 2006; Sonesson & Meuwissen 2000). However, to our knowledge the two methods have never been compared. Particularly, they have not been studied with respect to their performance in populations of zoo animals managed as herds.

Current analysis shows that breeding circles can be a good solution for small populations maintained in zoos. They can efficiently reduce inbreeding rate with minimum data input. It only requires information about herd of origin for each animal. This is sufficient to plan which individuals will be transferred to another herd. Therefore, the quality of pedigrees does not affect the performance of the breeding program (Windig & Kaal 2008). Moreover, simple organization of breeding circles makes them easy to set up. It could be relatively easy to determine which zoos would exchange animals and assign them to the breeding circle. Assignment of zoos to the breeding circle could be done considering their geographical locations so that animals are not transported over long distances. In case of populations where

the location and costs would prohibit the transfer of animals on a regular basis, the OC method supplemented with only occasional exchange could be a more feasible option. Additional research is needed to determine the sensitivity of rotational mating to such factors as overlapping generations, frequency and complexity of rotation pattern.

Rotational mating appears to be a very robust method that can restrict inbreeding regardless of selection pressure and pedigree completeness. However, caution is required when not all animals are used for breeding, as is the case for populations where excess males are culled or removed. Selection criteria in rotational mating schemes are not based on measures related to genetic diversity harboured by each animal (mean kinship or heterozygosity). It relies entirely on phenotypic selection which involves a risk of unintentional selection for “the best animals”; this may lead to genetic adaptation to captivity (Frankham 2008). This risk can be minimized by selection of males using criteria related to genetic diversity along with careful management of migration rates.

In the rotational mating schemes all of the selected males are assumed to contribute equally to the next generation. On the other hand, optimal contribution theory allows for optimizing their contributions and assigning different number of progeny to each male depending on their relatedness to the population. Therefore optimal contribution requires more control from species coordinators allowing for a more precise management of the population.

Apart from the management scheme used (optimal contribution or rotational mating), the major factor affecting inbreeding rate was population size. Our results demonstrate that populations with less than 60 animals cannot be managed without losing genetic diversity at an unacceptable rate. According to the analyses of programs run by AZA and EAZA more than a third of the populations are comprised of less than 50 individuals (Leus et al. 2011; Long et al. 2011). Therefore, in such small populations it is particularly important to

maximize the number of males that participate in mating. In the simulated populations, a mating ratio of 1:2 essentially always resulted in inbreeding rates below 1% per generation. Higher mating ratios (1:5 and 1:10), where a very limited number of males participated in mating usually led to a rapid increase of inbreeding regardless of the management scheme. This was particularly apparent in populations managed as isolated herds, though the problem exists also in herds with rotational exchange of males. Our results suggest that in a population with 240 animals spread over 6 herds, the rate of inbreeding can be restricted to <1% per generation. Therefore six zoos or deer parks could be sufficient to conserve an endangered population. This points towards the need to increase the size of populations that are considered as valuable form a conservation stand point.

The best results in terms of kinship and rates of inbreeding were obtained when OC was carried out within the meta-population. In the meta-population there are more parents, resulting in lower average relatedness. On the other hand, when the population is divided into isolated herds, a much lower number of parents is available, which translates into a significant increase of inbreeding. In isolated herds genetic drift reduces genetic diversity within herds (Frankham et al. 2010; Lacy 1987). When subpopulations become completely inbred, the total genetic diversity is preserved due to genetic variability between the herds (Lacy 1987). However, this approach poses a significant risk that some subpopulations will suffer from inbreeding depression, and may not survive (Leus et al. 2011). Moreover, sub-populations depart significantly from the founders (Chesser 1983). Therefore it is important to manage both the exchange of animals between the herds and contributions of animals from each herd to the next generation (Fernández et al. 2008).

Zoo populations usually have a very limited capacity that restricts the number of animals which can be kept in the population. Therefore, to maintain the populations in good condition and avoid overcrowded zoo environment, it is necessary to either transfer part of the animals

to another zoo or to cull them. In the latter case it is important to remove those animals that are least valuable to the population. The number of animals that have to be culled (selection intensity) depends on reproductive capacity of the species. Generally selection intensity will be higher in males than in females, which is similar to the conditions simulated in the current study, where mating ratio determined selection intensity. A selective culling strategy can also increase fitness of the population by eliminating individuals with health and fertility issues. The main goal of conservation programs is to select animals that are beneficial for genetic diversity of the population due to their low average relatedness to the population. One must also bear in mind that in certain cases also some unintentional selection for desired phenotypic characteristics may take place. This may lead to genetic adaptation to captivity which is undesirable from a conservation point of view (Frankham 2008). That is why in the current study, breeding scenarios were evaluated with respect to their potential to restrict inbreeding under no directional selection pressure and with unintentional selection. Our results indicate that by using a rotational mating scheme, inbreeding can be restricted with and without directional selection. However, any form of directional selection will increase adaptation to captivity and loss of "wild" alleles. Therefore the choice of selection criteria and breeding scheme is a crucial point in managing populations.

It is important to look at the current results in the light of assumptions made during the design of the simulations. One of the restrictions was that animals could reproduce only once in their lifetime and were replaced by their offspring thereafter (discrete generations). This assumption could be valid also in real zoo populations as long as females that had produced offspring were moved away from males. Otherwise, overlapping generations could be accounted for in the optimal contribution algorithm, and the average coancestry would be limited across generations (Meuwissen 1997). Another limitation of the simulated population was connected with reproductive capacity of females. To keep a constant population size, it

421 was assumed that dams always give birth to two offspring. Removing this restriction will
422 improve the performance of the OC algorithm. Additionally, to keep a constant population
423 size, each generation all females had to be used for breeding and selection was possible only
424 among males. In real populations, where generations overlap, it would be also possible to
425 perform some selection on the female side. Using the appropriate breeding scheme, this could
426 have a positive effect on fitness of the population without detrimental effects on the rate of
427 inbreeding (Meuwissen 2009). Results obtained with the investigated methods could be
428 further improved by optimisation of mating schemes. In the current simulations it was
429 assumed that the selected animals were mated at random. Use of a two stage optimisation
430 methods, where the optimisation of contributions is followed by optimisation of mating pairs,
431 could have a positive effect on the inbreeding level and the amount of genetic diversity
432 conserved (Ivy & Lacy 2012). Another alternative could involve a single-step optimisation
433 process, where both the contributions and mating design would be optimised in one step
434 (Fernandez et al. 2001).

435

436 Comparison of optimal contributions carried out in a meta-population and in a population
437 divided into herds, showed that breeding within isolated zoos leads to a significant increase in
438 inbreeding within individual herds. Optimal contribution method performed better when it
439 was conducted within a meta-population. However, due to organizational issues global
440 management of geographically separated herds can be a problem. Therefore, a combination
441 of the optimal contribution method with rotational mating might be a better alternative. In
442 this situation, optimal contribution method would be carried out separately within each herd.
443 Additionally, each generation males would be exchanged between the neighbouring zoos.
444 Comparison of optimal contribution method with rotational mating demonstrated that they
445 perform equally well. Simulations showed that rotational mating can efficiently reduce the

inbreeding rate. Moreover inbreeding rate in breeding circles with and without selection pressure was similar. Therefore unintentional selection does not reduce the efficiency of this scheme with respect to restriction of inbreeding. On the other hand, optimal contributions require more control over the conservation scheme by varying the contributions of animals to the next generation. However, optimal contribution requires complete and accurate pedigree records (Oliehoek & Bijma 2009), which are often unavailable (Mucha et al. unpublished results). Combination of the two methods (OCr) would result in a robust scheme which slows down the increase of inbreeding and works irrespective of the pedigree. Accompanied by optimization of animal contributions within each herd, this scheme would give further benefit depending on pedigree completeness and would not be sensitive to unintentional selection.

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545

546 **Table 1.** Selection criteria for males, their contributions to the next generation and exchange

547 between herds.

Scenario	Selection	Contributions	Exchange	Abbreviation
Rotational	Random	Equal contributions	Between herds	RM
	Mass			
Optimal contribution	Kinship	Optimal contribution theory	Across meta-population	OC_m
			Between herds	OC_r
			Within herds, no exchange	OC_i

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549

Table 2. Inbreeding rate (ΔF[1]), and mean kinship within and across herds after 20 generations of selection.

Population Size[2]	mating ratio	RM			OC_m		OC_i			OC_r		
		ΔF [%]	Kinship		ΔF [%]	Kinship	ΔF [%]	Kinship		ΔF [%]	Kinship	
			within[3]	across				within[3]	across		within[3]	across
3x20	1:2	0.83	0.19	0.16	0.71	0.14	2.20	0.38	0.13	0.75	0.18	0.15
	1:5	1.89	0.37	0.32	1.53	0.28	4.93	0.65	0.22	1.55	0.32	0.28
	1:10	3.24	0.55	0.49	3.11	0.48	10.99	0.91	0.30	3.14	0.54	0.48
6x40	1:2	0.22	0.08	0.04	0.17	0.04	1.02	0.20	0.03	0.19	0.07	0.04
	1:5	0.52	0.15	0.09	0.37	0.08	2.30	0.39	0.07	0.40	0.12	0.08
	1:10	0.93	0.26	0.16	0.72	0.14	4.74	0.64	0.11	0.76	0.22	0.14
20x60	1:2	0.13	0.05	0.01	0.03	0.01	0.72	0.15	0.01	0.12	0.04	0.01
	1:5	0.31	0.10	0.02	0.07	0.02	1.53	0.28	0.01	0.24	0.09	0.02
	1:10	0.58	0.18	0.04	0.14	0.03	3.09	0.48	0.02	0.45	0.15	0.03

[1]Mean increase of inbreeding in generations 5 to 20; [2]nr of herds x nr of animals in each herd; [3]kinship calculated within each herd. OC_m, OC_i OC_r and RM, see table 1.

Table 3. Genetic level, and inbreeding rate in breeding circles with and without random selection of males.

Scenario	mating ratio	Not random		Random	
		G[1]	ΔF[2]	G[1]	ΔF[2]
Three herds with 20 animals per herd	1:2	1.78	0.84	0.04	0.83
	1:5	2.64	1.91	0.05	1.89
	1:10	2.55	3.25	0.03	3.24
Six herds with 40 animals per herd	1:2	1.98	0.23	0.00	0.22
	1:5	3.18	0.53	0.00	0.52
	1:10	3.41	0.94	-0.01	0.93
Twenty herds with 60 animals per herd	1:2	2.01	0.14	-0.01	0.13
	1:5	3.34	0.33	-0.02	0.31
	1:10	3.79	0.61	-0.01	0.58

[1]G – mean genotypic level of the population after 20 generations of selection, expressed in units of standard deviation from the mean of the founder generation.

[2]ΔF – inbreeding rate in %

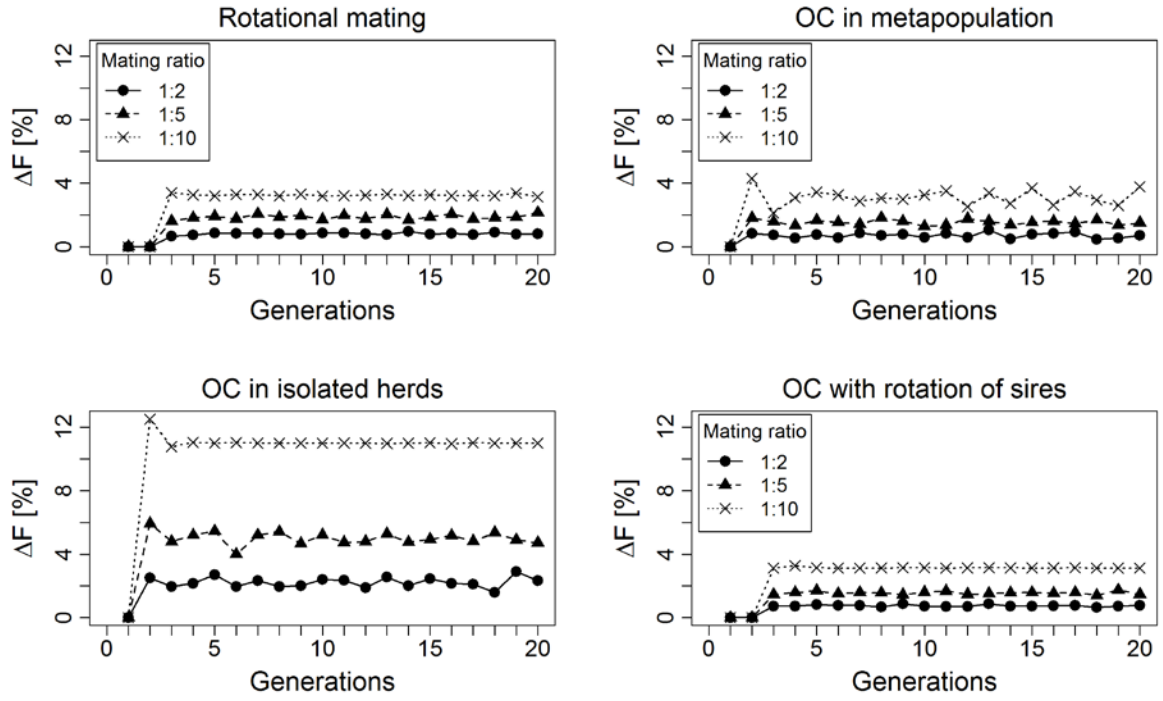

Figure1. Inbreeding rate in population of 60 animals, divided over 3 herds, managed with different scenarios